sorogenesis may be readily shifted by altering the light and dark periods. Soro carps that develop in culture dishes placed in a dark box with light entering from a small opening on one side show no tendency to become oriented toward the light source.

The information presented here should facilitate more detailed developmental studies of this unique ciliate.

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Chimpanzee Problem-Solving: A Test for Comprehension

Abstract. *An adult chimpanzee was shown videotaped scenes of a human actor struggling with one of eight problems and was then shown two photographs, one of which depicted an action or an object (or both) that could constitute a solution to the problem. On seven of the eight problems, the animal consistently chose the correct photograph. This test of problem-solving comprehension permits the animal's knowledge about problem-solving—its ability to infer the nature of problems and to recognize potential solutions to them—to be examined.*

Köhler's pioneering experiments on tool use by chimpanzees provided early evidence for complex problem-solving capabilities in a nonhuman species. The chimpanzees, when faced with inaccessible food, fit sticks together for use as a rake, propped up poles or stacked boxes for use as ladders, pulled strings attached to distant goal objects, and moved aside physical obstructions blocking their paths (*1*). Subsequent research by other investigators has focused on behavioral mechanisms of the ape's performance. For example, many of the actions chimpanzees display in problem situations can be traced to "innate" origins in play behavior, and the behavioral progression from apparently random activity to organized, goal-directed solution behaviors may often be described in terms of trial-and-error learning (*2*). However, Köhler noted that some of his subjects arrived at solutions quite suddenly, after a period of intense activity and then quiescence. He proposed that such cases revealed "insight"—perceiving relationships between a problem and its solution—which organized successful goal-oriented behavior. Unfortunately, these intriguing observations have received little experimental attention in subsequent research.

To what extent does the chimpanzee comprehend the elements of a problem situation and potential solutions? Our understanding of this aspect of problem-solving in chimpanzee and other species is limited by methods that rely solely on observations of subjects producing solutions to problems. It is essential to study not only the animal's problem-solving performance but also its knowledge about problem-solving. Accordingly, we designed a procedure which provided a chimpanzee with the opportunity to observe, rather than participate in, a problem situation. We simply showed the subject videotaped scenes of a human actor encountering one of several problems. The chimpanzee was then required to identify, rather than produce, a means for solving the actor's problem by choosing a photograph depicting a potential solution. By this technique, we examined the chimpanzee's capacity to recognize representations of problems and solutions, as well as its ability to perceive the relationship between each type of problem and its appropriate solution.

The subject was Sarah, an African-born female chimpanzee (*Pan troglodytes*) approximately 14 years old. She was obtained by the laboratory when less than 1 year old and was trained and tested on numerous cognitive tasks, including a simplified language (*3*). Although she had no formal experience with the problems investigated here, she did have extensive prior exposure to photographs and television programs broadcast over commercial networks, a factor which undoubtedly contributed to her performance with the visual test material.

The test consisted of two tests with four problems each. For each test, we staged one 30-second scene of a trainer struggling with each of four problems and videotaped each scene. In addition, we made photographs of either the trainer performing an action with an object or an object alone, which could constitute a solution to each problem. The two tests differed in the nature of the televised problems and in the content of the photographic solutions. In test 1, problems were of the standard variety used in animal testing and were based on those Köhler arranged for his chimpanzee subjects (Fig. 1) (*1*). Videotaped scenes showed the actor struggling to reach bananas made inaccessible in one of four ways. The photographic solutions depicted the actor performing an action with an object in the situation. In test 2, a new set of problems was drawn from events in the daily laboratory routine, and the photographic solutions merely showed objects which could constitute a solution to each problem. In this second test, "problem" was no longer defined simply as inaccessible food but ranged from a human actor locked inside a cage to a gas heater that had gone out (Fig. 2).

Each test consisted of several daily sessions of four trials each, with intertrial intervals of approximately 2 minutes. During each trial, Sarah was shown one black-and-white videotaped scene on a television monitor (Sony CVM-115 with an 11-inch screen). In the last 5 seconds of the scene, the videotape was put on "hold," thereby leaving an image of the problem situation on the screen like one of those shown in the left-hand columns of Figs. 1 and 2. The trainer then handed Sarah a covered box containing two of the set of four 8- by 10-inch color photographs, each mounted on a 10- by 12-inch piece of plywood. Afterward, the trainer left the room and closed the door. Sarah was required to open the box, select one photograph, and place it on a paper towel in front of the television screen. This aspect of the procedure was derived from a previous match-to-sample paradigm, in which Sarah was trained to place correct comparison stimuli on a towel and incorrect ones elsewhere. Sarah then summoned the trainer from an adjacent room by ringing a bell. Thus, the subject responded in the absence of the trainer, a procedure we use routinely for the control of social cues (*4*). When the trainer heard the bell, he returned to the test room and graded Sarah's answer, telling her either "Good Sarah, that's right," or "No Sarah, that's wrong," in a tone of voice one would use with a young child. At the end of every session she was given yogurt, fruit, or candy.

Before each test, Sarah was given a preliminary session in which she was shown the set of four videotaped scenes in order to familiarize her with the test material. During subsequent sessions in each test, she was shown all four scenes, one at a time, and then asked to choose one of two photographs at the end of each scene. The order in which the scenes were presented was randomized across sessions, and the position of the correct photograph inside the box (left versus right) was counterbalanced across trials. On all trials, one photograph was correct and the other incorrect, and each correct alternative was paired equally often with every other alternative. Tests 1 and 2 consisted of six and three daily sessions, respectively.

In both tests, Sarah chose correctly on a significant proportion of the trials (21 of 24 trials correct in test 1, binomial test, $P < .001$; and 12 of 12 trials correct in test 2, $P < .001$). In the first test, she chose the correct photographic solution on all six presentations of the first three problems. Her errors were confined to problem 4, in which the trainer's access to food was hindered by a block-laden box (Fig. 1). She chose incorrectly on the first three trials with this problem and then chose correctly on the last three trials. Her incorrect choices were, in order of occurrence, reaching out with the rod, stepping on the box, and pushing the box laterally. It may be noted that Sarah's difficulty with problem 4 is in keeping with Köhler's observation that his chimpanzees solved this kind of problem only with great difficulty, if at all (*1*). Thus, although Sarah may have learned during the course of test 1 to choose the correct photographic solution to problem 4, this would be an improbable interpretation of her overall performance. On problems 1, 2, and 3 in test 1 and in all four problems in test 2, Sarah performed without error from the outset of testing. Examining the data from her first trial with each problem (which eliminates the possibility of learning), showed that she chose correctly on a significant proportion of problems upon first exposure (seven of eight correct initial choices, binomial test, $P < .05$).

These results demonstrate that the chimpanzee was capable of bringing representations of problems and solutions into correspondence with one another. The subject's success suggests not only that she recognized that the videotaped scenes represented problems (that is, actions or conditions the human actor was unable to realize) and the photographs represented potential solutions (means by which the actor's goal could be achieved), but that she perceived the relationship between each type of problem and its appropriate solution. Quite how the chimpanzee carries out this task remains to be determined, although some alternatives can already be eliminated.

The problems could not be solved by matching videotaped scenes and photographs on the basis of physical similarity. In test 1, each video scene showed the trainer, bananas, rope, a box, a rod, and two cement blocks; and each photograph showed the trainer and either one, or in the case of the fourth problem, two of the objects. Test 2 further discounts this possibility, for there is no physical similarity whatever between, for example, a key and an actor struggling to escape from a cage, or between a flaming torch and an actor "registering" cold. Alternatively, one might suppose that not objects but the actor's posture was a basis for physical matching. In test 1 he is decidedly more upright in the first problem and its solution than in the other pairs of stimuli. Yet this would differentiate only one problem from the oth-

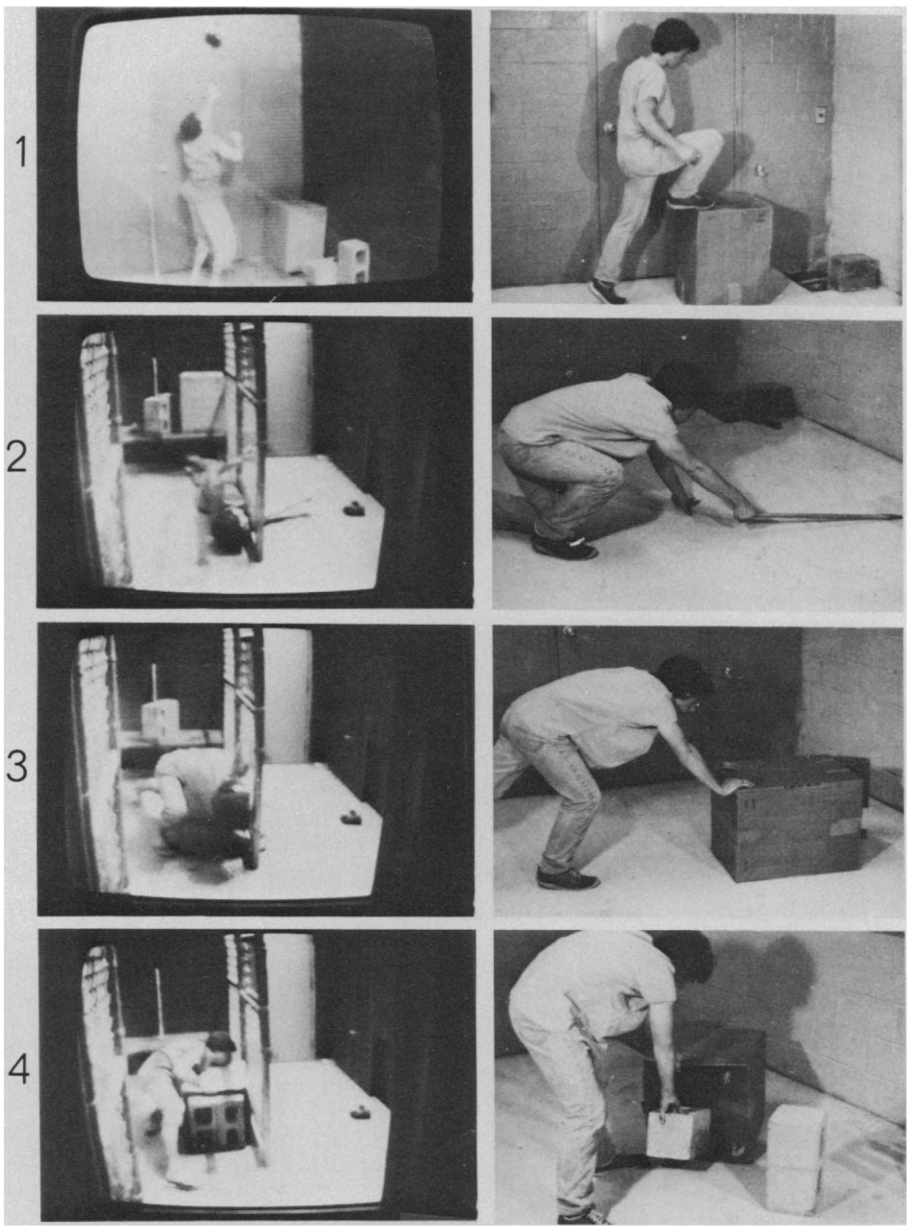

Fig. 1. Photographic reproductions of the four televised problem scenes in test 1 (left column) and of the color-photograph solutions (right column). Photographs of the television monitor in the left column were taken during the last 5 seconds of each 30-second videotaped scene. The correct means for solving each problem is portrayed in the photograph directly to the right of each problem scene. In problem 1, the trainer attempted to reach up toward bananas suspended by a rope from the ceiling; in problem 2, to reach under the wire mesh partition toward bananas on the floor; in problem 3, to reach around an intervening box toward bananas on the floor outside the cage; and in problem 4, to push aside a box filled with cement blocks, which obstructed his reach toward bananas on the floor outside the cage. In solution 1, the trainer stepped on a box; in solution 2, he reached out with a wooden rod; in solution 3, he pushed laterally on a box; and in solution 4, he lifted blocks out of a box.

er three and thus would not account for the results. Posture may be one of several cues the animal uses to identify a problem, provided it is available, but the results of test 2 show that it is not a necessary cue. Although the photographs in test 1 depicted a trainer acting on an object (and thus assuming a posture), those in test 2 did not depict an actor at all but merely showed either an object that could serve as a tool (key, flaming torch) or objects in an appropriate combination (cord plugged into a socket, hose connected to a faucet). To account for Sarah's performance we must appeal to a level of analysis deeper than physical similarity of the stimuli.

Did Sarah's prior experience, either personal or observational, mediate her successful performance here? To our knowledge, she has never observed a human or conspecific encounter the types of problems investigated in test 1. However, she is almost certain to have had informal experience with some of them. It is hardly possible to prevent a chimpanzee from engaging in daily problem-solving (as Köhler noted, the "official" problem-solving he observed was not the first problem-solving in which his subjects had engaged). Sarah has obtained items lying outside her cage by reaching with a variety of objects, climbed on objects in her cage in order to grasp items on the ceiling, and even in these tests, removed the lid on the box in order to gain access to the photographic alternatives. However, the inaccessible items she reached toward were never bananas, but rather keys or articles of clothing. Her "tools" were never rods or boxes, but furniture, toys, or blankets. Physical obstructions were never boxes in her cage, but rather lids on small containers or large surfaces such as the cage walls. And, of course, the agent who participated in the problems was not the trainer, but Sarah herself. Nevertheless, her own experience differed only in detail from that represented by each of the first three problems in test 1, and this may have been the basis of her success. In contrast, we doubt whether she had any personal experience with the kind of problems depicted in problem 4. Owing to her great strength, she has probably never encountered a small object she could not move, and her failure on the fourth problem may stem from a lack of personal experience.

On the other hand, observational learning must have played an important role in Sarah's performance in test 2. Although she has used keys (problem 5) adeptly on several occasions, she has had no personal experience like that represented in problems 6, 7, or 8. She has observed trainers ignite gas heaters, attach hoses to faucets, and plug in electric cords, but she has never carried out these acts herself. Moreover, her observational experience with these activities was casual, a part of the daily routine. For example, she did not observe a trainer attempt to play the phonograph, fail, and then notice belatedly that the cord was not plugged in. None of the acts were ever staged for her benefit, the separate parts of the acts such as the plugging in of the cord or the attachment of the hose being highlighted in a didactic way.

The exact experience the subject needs in order to perform as Sarah did, the critical features of the problem scenes and photographic solutions, and how these factors for nonhuman species compare with those needed by the human child remain to be determined. Further research may answer these ques-

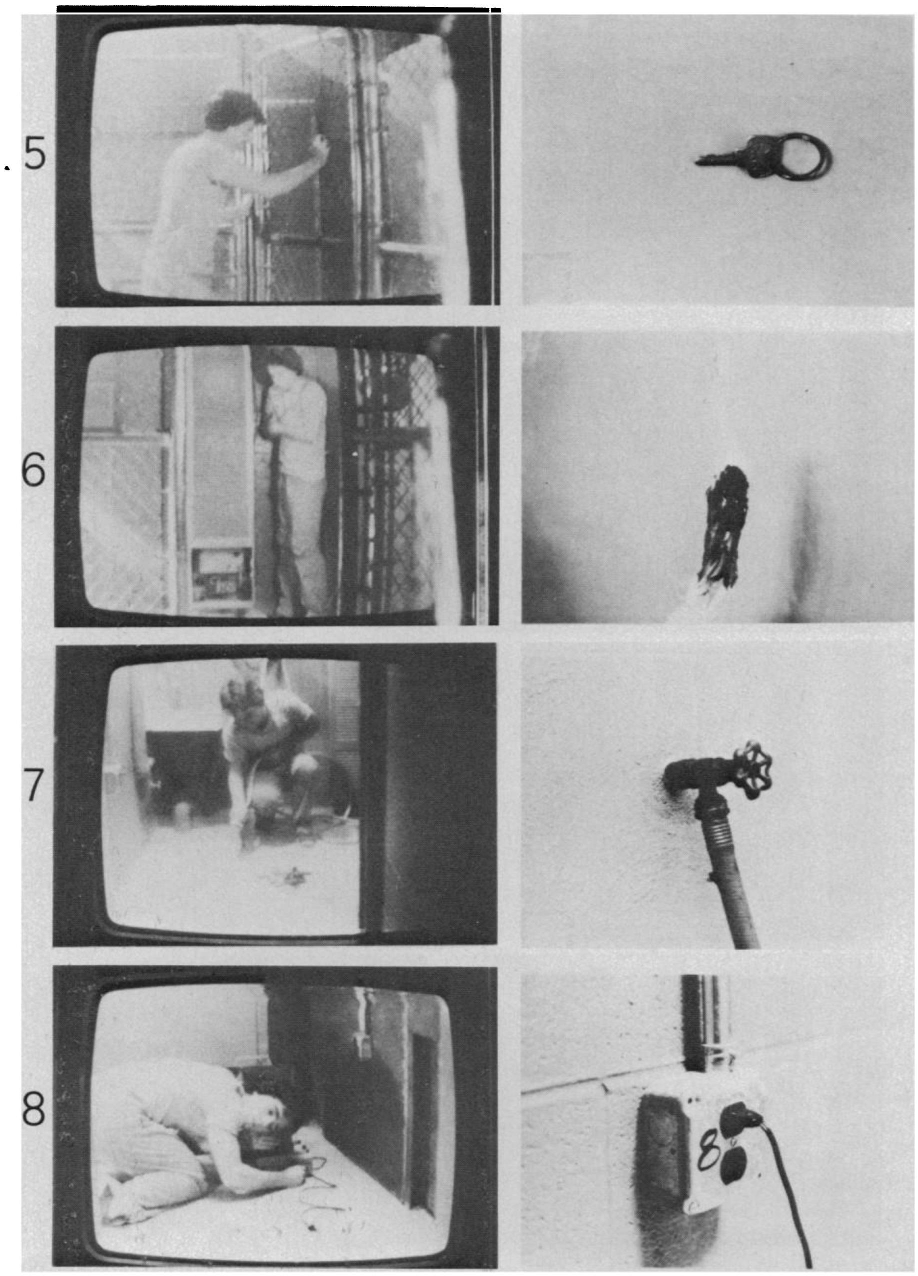

Fig. 2. Photographic reproductions of the four televised problem scenes in test 2 (left column) and of the color-photograph solutions (right column). Photographs of the television monitor in the left column were taken during the last 5 seconds of each 30-second videotaped scene. In problem 5, the trainer struggled to escape from a locked cage, alternately grasping the bars of the cage and the padlock on the door; in problem 6, he shivered, clasped his arms to his chest, and slapped the gas heater on the wall; in problem 7, he attempted to wash down a dirty floor, but the hose was not connected to the faucet; and in problem 8, he attempted to play a phonograph record, but heard no sound because the machine was not plugged in. The photographs on the right show, for solution 5, a key on a key ring; for solution 6, a torch in flames; for solution 7, a hose connected to a faucet; and for solution 8, a plug connected to a wall socket.

tions and generally enhance our knowledge about the degree to which nonhuman species and young children understand their own problem-solving behavior.

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Taste Responses in Sheep Medulla: Changes During Development

Abstract. *Response characteristics of taste neurons in the sheep solitary tract and nuclei alter during development. Solitary tract cells in younger fetuses respond to stimulation of the tongue with fewer salts and acids than do cells in older fetuses, lambs, and adults. Further, responses to specific salts and acids develop in a particular sequence, not randomly. These changes may relate to maturation of taste receptor sites.*

Taste buds appear on the mammalian tongue early in development, at about one-fifth of gestation in the human fetus (*1*) and one-third of gestation in fetal sheep (*2*); studies on sheep have shown that fetal taste buds respond to chemical stimuli (*2*). In earlier experiments to determine whether neurophysiological taste response characteristics alter as the taste system matures, we recorded summed chorda tympani nerve responses to chemical stimulation of the tongue in 100- to 147-day (term) sheep fetuses (*2*). Fetal receptors were comparable to those of newborns and adults in that they responded to a variety of stimuli, including a wide range of NH_4Cl concentrations. More recently, recording from the central nervous system has enabled us to study the taste system in younger fetuses and to obtain more single- and few-unit neural responses (*3*). We now report changes in taste responses recorded from the solitary tract and nuclei (ST) in sheep fetuses from 84 days of gestation to term, in lambs, and in adults.

To record taste responses in fetal sheep, a pregnant ewe of known gestational age is anesthetized with sodium pentobarbital, and the fetus is delivered (*2*). The fetus remains attached to the maternal circulation throughout the experiment and can be maintained with stable internal temperature and heart rate for 4 to 16 hours (heart rate usually becomes erratic after 4 to 6 hours in fetuses between the ages of 80 and 95 days of gestation).

The fetal head is flexed at a right angle to the body and secured in specially designed head bars; sponges under the neck provide additional support. The cerebellum is removed by aspiration to reveal the floor of the fourth ventricle, which is then covered with mineral oil at 38°C. Coordinates for the position of the ST are determined from previously prepared sections of fetal brains at different gestational ages. Commercially made tungsten microelectrodes, with impedances ranging from 3 to 15 megohms and an exposed tip of < 1 μm are used to record neural activity. With the obex as a reference point, the electrode is positioned and advanced into the brain through the use of a three-coordinate microelectrode holder. Neural activity is amplified by a differential a-c preamplifier and monitored with an oscilloscope and audioamplifier. The neural activity is recorded on one channel of a magnetic tape recorder; voice cues are recorded on a second channel to provide information on experimental procedure.

As the microelectrode is driven through the medulla, units are located by applying frequent tactile and chemical stimuli (0.5*M* NH_4Cl or KCl) to the anterior tongue (approximately 30 percent of total tongue length). When a responsive unit is found, the tongue is stimulated with 20 ml each of 0.5*M* NH_4Cl, 0.5*M* KCl, 0.5*M* LiCl, 0.5*M* NaCl, 0.1*M* citric acid, and 0.01*N* HCl. Solutions are applied from a syringe, remain on the tongue for at least 20 seconds, and are then rinsed from the tongue with distilled water for 30 to 60 seconds. To monitor the reproducibility of the response, 0.5*M* NH_4Cl is used as every third or fourth stimulus. All chemicals are dissolved in distilled water and maintained at room temperature during experiments.

For comparative purposes, recordings from chemosensitive units are also made in the ST of lambs and adult sheep. Procedures for exposing the ST and recording from neurons are similar to those used in fetuses.

Twenty-three single- or few-unit recordings (*4*) were made in the ST while stimulating the tongues of 17 fetuses between the ages of 84 and 126 days of gestation. Ten single- or few-unit recordings were made in six lambs 42 to 82 days old, and nine recordings were made in five adult sheep. Electrolytic lesions were made after recording chemosensitive responses from 16 fetal and two lamb units; sites were located in the rostral region of the ST, extending from the level of incoming glossopharyngeal (ninth) nerve fibers to the level of incoming intermedius (seventh) nerve fibers.

Histograms of neural frequency before, during, and after chemical stimulation of the tongue were obtained by converting neural activity to standard pulses and counting the pulses with a rate meter. These histograms were analyzed to determine whether or not a response occurred during stimulation of the tongue with each of the six chemical stimuli. A response was defined as an increase in mean impulse frequency greater than the mean plus 2 standard deviations of the spontaneous discharge frequency for that unit (*5*).

With increasing age, ST units responded to a broader range of stimuli (Fig. 1). For example, almost half the units in fetuses responded to only three of the six stimuli. Only about one-tenth of fetal units responded to all six chemicals, whereas in lambs and adults, almost six-tenths responded to six. However, the transition to a broad responsive range was gradual, and any partition of units according to age groups is somewhat arbitrary.

A broad responsive range of chemosensitive neurons is characteristic of the adult taste system in other species. Doetsch and Erickson studied responses of rat chorda tympani fibers and ST cells to 14 stimuli, including ten salts and two acids (*6*). They reported that both first- and second-order taste neurons responded to "most" of the stimuli used.

Figure 2 illustrates responses from two or three "narrowly" responsive, 105-day fetal sheep units, compared with those from a "broadly" responsive, 122-day

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